SIGNIFICANCE OF THE LATE PLEISTOCENE FAUNA FROM THE LITTLE BOX ELDER CAVE, WYOMING, TO STUDIES OF ZOOGEOGRAPHY OF RECENT MAMMALS

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ABSTRACT.—A late Pleistocene mammalian fauna from Little Box Elder Cave, eastern Wyoming, provides paleontological evidence bearing on several contemporary and related studies in zoogeography of Recent intermontane mammals and on understanding of rapidly changing environments in the Rockies in late Pleistocene and post-Pleistocene time. Both paleontological and zoogeographical findings suggest that during glacial periods in the Pleistocene the life-zones were lowered and, therefore, many boreal mammals ranged away from the glaciated Rocky Mountain chain. Since then, some of these returned or retreated northward as the climate moderated, and many warmth-adapted mammals approached the Rockies. The fossil and Recent faunas analyzed together reveal that the post-Pleistocene climate became so warm that numerous boreal species disappeared from habitats that are now again boreal (montane). Some warmth-adapted species have advanced to and retreated from the cave area. The climatic optimum, as well as the glacial and interglacial periods, apparently affected the distribution of numerous mammals in this area.

Introduction

The Central Rockies and the lower, warmer prairies of the Great Plains to the eastward have been intensively investigated by biologists and geologists. The biologists have ascertained the geographical distribution of much of the Recent biota, and the geologists, especially the Pleistocene geomorphologists, have postulated a climatic history for this region. However, a great hiatus in the evidence available for zoogeographical studies of intermontane mammals has been the paucity of information on late Pleistocene fossil deposits in this region.

A faunal list (Anderson, 1968), completed it seems in 1964, records late Pleistocene mammals from Little Box Elder Cave, Converse County, Wyo., and substantiates and augments several contemporary studies on the zoogeography of Recent mammals. The fossil remains from this cave are discussed below concerning the distribution and speciation of mammals of the Central Rockies, the Black Hills, the Bighorn Mountains, the northern ranges of the Southern Rockies, and the plains of eastern Wyoming and western Nebraska.

GENERAL ECOLOGY AND MAMMALIAN ZOOGEOGRAPHY OF THE REGION

The habitat at Little Box Elder Cave is semiarid; the vegetation is reportedly comprised of sagebrush, grama grasses, ponderosa (yellow) pine, narrow-leafed cottonwood, box elder, mountain mahogany, skunk-brush (*Rhus trilobata*), poison oak, prickly pear, and lichens (Anderson, 1968:51). This habitat would be in the Transition Lifezone judging from such plant indicators as sage, yellow pine, and

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narrow-leafed cottonwood (Cary, 1917). The cave is in the Laramie Mountain system, some peaks of which are covered by coniferous forest. Long (1965:725) ascribed the forested hills near the cave to the Laramie Mountains Faunal Subdivision, the warm lowlands to the Cheyenne Plains Faunal Division of the Great Plains Faunal Area (see below). Clark (1970) recently discussed the ecology of

this semiarid division.

The general ecology of Wyoming was discussed by Merrit Cary (1917) and reviewed by Long (1965). The life-zone concept clarifies the profound effects of temperature ranging from the cold, wet Arctic-alpine Life-zone down to the hot, arid Upper Sonoran Life-zone. The highest elevation in Wyoming is 13,785 ft, and the lowest 3100 ft, in the valley between the Bighorn Mountains and the Black Hills. The annual precipitation varies from well over 20 inches in the western and southern mountains to less than 10 inches in the lowest valleys and basins. An elevated base level in Wyoming, about 6000 ft, is related to generally cool climate, averaging 10 F cooler in the mountain valleys than on the plains.

The differential effects of climate categorized by the life-zones in Wyoming are reflected in the vegetation zones (Cary, 1917; Long, 1965). Many Wyoming mammals (especially subspecies) show association with either boreal or lowland plants. The boreal habitats in the Central Rockies today are confined to the high mountain ranges and comprise the forested Canadian and higher life-zones (Fig. 1). Sage, grasses, yellow pine, and other plants of the lowlands

indicate the Transition and lower life-zones.

Owing to weaknesses in the life-zone concept (see Kendeigh, 1954; Long, 1965), it was augmented in Wyoming (Long, 1965) by the concept of faunal areas and their subdivisions based on mammalian distributions (Fig. 2). Faunal areas were used by Grinnell (1914) to depict natural faunistic assemblages delimited by relative humidity. This concept was modified by Durrant (1952) to categorize areas simply by the presence or absence of certain mammals. Durrant's approach explains the composition of faunas that reflect both present and past environmental factors, and his method has been used by several workers in the intermontane states.

The geographical ranges of mammals of Wyoming were ascertained (Long, 1965) by study of nearly 13,000 preserved specimens. Jones (1964) determined the geographic distributions of nearby Nebraskan mammals after studying thousands of specimens over a period of 15 years. The concept of faunal areas in the cave area rests on a basis of intensive and long-continued field investigation.

Most of the high mountains in Wyoming lie along or west of the Continental Divide and comprise the Rocky Mountain Faunal Area (Fig. 2). The mountains for the most part are massed in both northwestern and south-central Wyoming. An arid, low discontinuity between these mounainous areas includes the Central Portal Faunal Area and the Upper and Lower Green River divisions (of the Rocky Mountain Faunal Area). The Great Plains, found eastward of the Rockies, comprise the Great Plains Faunal Area. The plains isolate

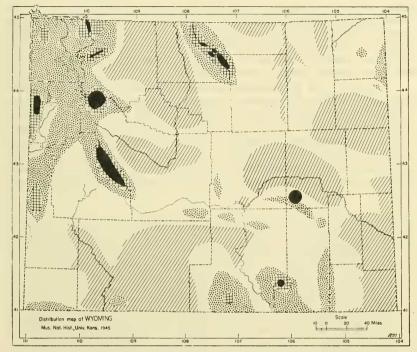


Fig. 1. Geographic distribution of life-zones of Wyoming. Black areas, Arctic-alpine. Hatched areas, Hudsonian. Stippled areas, Canadian. Clear areas, Transition. Lined areas, Upper Sonoran. The black dot is the locality of Little Box Elder Cave.

the Bighorn Mountains, and especially the Black Hills, from the Rocky Mountain chain. Some lowland species and subspecies range across the Continental Divide through the low Central Portal Faunal Area. The Wyoming faunal divisions and subdivisions (Fig. 2) and the mammals that inhabit them are more fully discussed by Long (1965:726-729). The Wyoming mammalian fauna consists primarily of montane species and subspecies more or less restricted to the Rocky Mountain Faunal Area, and of lowland species and subspecies inhabiting the deserts and basins in the west and the tremendous grassy prairies in the east.

When patterns of Recent distribution are found that are inconsistent with the ecological distributions resulting from the prairies and mountains, the reason may be that some ecological conditions today are different from those in the Pleistocene. Analysis of past climate provides understanding of the former environments and hence of unusual Recent patterns of mammalian distribution.

The history of climatic conditions in the Central Rockies is known, for the most part, from studies of past glaciations. The evidences were reviewed by Long (1965), Ray (1940), Holmes and

Moss (1955), and others. Briefly, the climate varied from cold, wet periods when glacial ice scoured the mountains and deposited moraines to warm, dry periods resembling present time when the ice receded or disappeared. The distances between cirques and terminal moraines reveal the extent of past glaciation, and the erosion of the moraines permits them to be correlated in regard to approximate age.

In general, the glaciations represented by moraines in the Rockies became decreasingly severe. Some inextensive formation of glacial ice has been aged as Recent, beginning about 2000 years ago, and numerous glaciers exist today especially in the Wind River Mountains (Wentworth and Delo, 1931). In the Central Rockies generally only the ancient and highest (Hudsonian and Arctic-alpine lifezones) mountain systems were glaciated (Fig. 1), although during early (severe) glaciations ice tongues descended into the lowlands

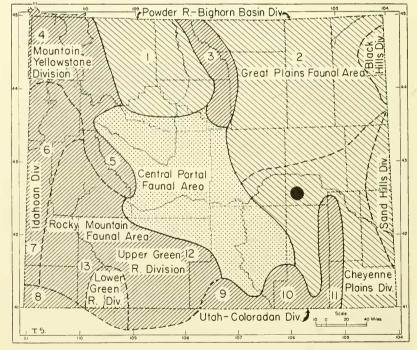


Fig. 2. Faunal Areas and Faunal Divisions of Wyoming (from Long, 1965). The dot shows the location of Box Elder Cave. Faunal areas are Rocky Mountain, Great Plains, and Central Portal. The Black Hills, Sand Hills, and Cheyenne Plains divisions are mentioned in the text, and the faunal subdivisions mentioned in this paper are identified as follows:

- 2 Powder River
- 5 Wind River Mountains
 5 Wind River Mountains
 11 Laramie Mountains
 13 Upper Green River
- 8 Uinta Mountains
- 10 Medicine Bow Mountains (=Snowy Range)

east of the Wind River and Absaroka ranges, into Jackson Hole, around the Bighorn Mountains, and north of the Uinta Mountains (Fig. 2). Low margins of glaciation were 6200 ft in the Bighorn Mountains, 8100 ft in the Medicine Bow Mountains, and 7500 ft in the Cache la Poudre area in Colorado. The Arctic-alpine Life-zone was perhaps several thousand feet lower than at present, and the other life-zones likewise were lower or absent.

Mammals now confined to montane areas probably dispersed freely (except on the ice masses and snowfields) when cool habitats were more extensive. These boreal mammals probably followed the rising life-zones upward in the montane areas during warming trends and were then replaced in the warm, arid lowlands by warmth-adapted species. These doubtless came from refugia eastward (e.g., Lepus californicus, Fig. 3) and westward of the Rocky Mountains. Some boreal species (e.g., Gulo, Erethizon) perhaps lived in Wyoming even during severe glaciations (Long, 1965).

The montane populations isolated today are not the only distributions that indicate lowered life-zones in the past, but they are the most impressive. The snowshoe hare, Lepus americanus seclusus, of the forested Bighorn Mountains (Fig. 3) shows stronger affinity to L. a. americanus occurring far to the northward than to the nearby L. a. bairdii of the Rockies (Baker and Hankins, 1950; Long, 1965). A relict population of golden-mantled ground squirrel, Spermophilus lateralis lateralis, occurs in the southern Wind River Mountains (Fig. 2) and intergrades with S. l. castanurus northward (Fig. 4). S. l. lateralis is widespread in the mountains southward beyond the arid Upper Green River Faunal Division in southern Wyoming and in Colorado. This discordancy in the distribution of S. l. lateralis suggests that its habitat was formerly more continuous from the Wind River Mountains into Colorado.

A pollen record (Hansen, 1951) reveals that in postglacial time the now warm Upper Green River Faunal Division was forested with boreal conifers, which were replaced by grasses, composites, and sage. S. l. wortmani occurs today in this arid area in suitable habitat (conifers on the north slopes of buttes). This subspecies closely resembles S. l. lateralis except for much paler pelage. Pale pelage is characteristic of many desert mammals (Gloger's Rule). Spruce forest also occurred lower than at present east of the Rockies, in the Nebraskan sandhills, approximately 12,600 years ago (Watts and

Wright, 1966).

If the distributions (Figs. 3, 4) of *Lepus americanus* and *Spermophilus lateralis* result from post-Pleistocene environmental changes, the distributions provide probable rates of evolution. *L. a. seclusus* and *S. l. wortmani* possibly evolved in less than 11,000 years.

Prairie distributions also support the theory of lowered life-zones. Except for the low Central Portal Faunal Area, the Rockies seem to separate numerous closely related pairs (Long, 1965). These, termed east-west pairs, are far more numerous (Table 1) than the north-south pairs (boreal mammals) separated by the Central Portal Area and Upper Green River Faunal Division (Findley and Anderson,

Table 1. List of east-west pairs of closely related taxa. The species indicate profound geographic isolation in the past, as do the numerous pairs. The list is updated from the discussion in Long (1965), incorporating recent range extensions.

Interacting as species in Wyoming

1. Sylvilagus floridanus S. nuttallii

2. Spermophilus richardsonii S. armatus

3. Cynomys leucurus C. ludovicianus

4. Perognathus flavescens P. fasciatus

5. Spilogale putorius interrupta S. p. gracilis

One species in Wyoming, another westward

1. Vulpes velox V. macrotis

Distinct taxa, possibly acting as good species

1. Sorex vagrans vagrans S. v. obscurus

2. Peromyscus maniculatus nebrascensis P. m. artemisiae

3. Clethrionomys gapperi galei C. g. brevicaudus

Subspecies groups

1. Eutamias minimus (large size)
E. minimus (small)

2. Spermophilus tridecemlineatus (large) S. tridecemlineatus (small) Subspecies pairs

Sorex cinereus haydeni
 c. cinereus

2. Reithrodontomys m. dychei R. m. megalotis

3. Microtus pennsylvanicus insperatus M. p. pullatus

4. Ondatra zibethicus cinnamominus O. z. osoyoosensis

5. Erethizon dorsatum bruneri E. d. epixanthum

6. Canis latrans latransC. l. lestes7. Vulpes vulpes regalis

V. v. machrourus

8. Mustela vison letifera

M. v. energumenos
9. Taxidea taxus taxus

T. t. jeffersonii 10. Odocoileus virginianus dacotensis

O. v. ochrourus

11. Bison bison bison
B. b. athabascae

12. Ovis canadensis audubonii O. c. canadensis

1956; Long, 1965). The species level of differentiation attained by several of the east-west pairs (including Spilogale putorius gracilis, S. p. interrupta; Sylvilagus floridanus, S. nuttalii; Perognathus fasciatus, P. flavescens; Spermophilus richardsonii, S. armatus; and others) suggests their isolation in the past by the lowered life-zones of the glaciated Rocky Mountain chain.

The Little Box Elder Cave is found at the eastern margin of the Rockies and at the western margin of the Great Plains (Fig. 2). The mammalian zoogeogaphy of these plains in nearby Nebraska was discussed by Jones (1964); the major alpine glaciations mentioned above for the Rockies are probably correlative with the late continental glaciations that Jones hypothesized as important in Nebraska.

According to Jones (1964) one needs to look no further back than the Wisconsin glaciation to explain the composition of the Recent mammalian fauna of Nebraska. He considers the Wisconsin advance (18,000 BP) and the Valders readvance (10,000-11,000 BP) as cold, wet periods related to a climate cooler than present. There probably were at that time in Nebraska some biotic assemblages seen today in more northern regions. Dillon (1956) suggested that at

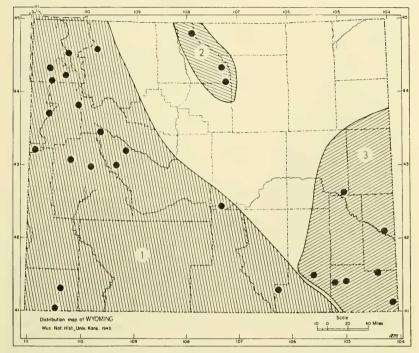


Fig. 3. Distribution of Lepus americanus and L. californicus: 1, L. a. bairdii; 2, L. a. seclusus; 3, L. californicus. Explanation in text.

the height of the Wisconsin glacial advance the Canadian Life-zone, characterized by conifers and aspen, was the warmest life-zone in Nebraska. Subsequently the climate in Nebraska moderated and warmth-adapted biotas approached the Rockies from the east. Jones (1964) suggested that the climate became so warm (the climatic optimum) after the Valders retreat (following the peak of Wisconsin glaciation) that some mammalian distributions in Nebraska were markedly affected. Populations of the short-tailed shrew, Blarina brevicauda, were separated. The pack rat, Neotoma floridana, ranged northward to the border of South Dakota, where a relict population now occurs.

LITTLE BOX ELDER CAVE

The entire faunal list of the mammals found so far in the cave and reported by Anderson (1968) need not be repeated here. The fossil remains evidently were deposited from late Wisconsin time to the present, comprising a mixture of boreal and warmth-adapted forms. The assemblage appears diverse; the sample, adequate for interpretation.

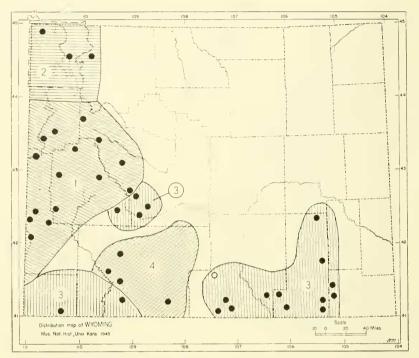


Fig. 4. Distribution of golden-mantled ground squirrels in Wyoming: 1, Spermophilus lateralis castanurus; 2, S. l. cinerascens; 3, S. l. lateralis; 4, S. l. wortmani.

Order Insectivora.—Fossil shrews not represented in the Recent fauna (Long, 1965) are Cryptotis sp. and Microsorex hoyi. Cryptotis parva today occurs along the Platte River as far west as Keith County, Neb. (Jones, 1964), and apparently has withdrawn its geographic range from the Laramie Mountains in eastern Wyoming. This finding certainly substantiates Jones's hypothesis that some species (e.g., Neotoma) have retreated since the climatic optimum. Microsorex hoyi was found in the northernmost Rockies of northern Colorado by Lechleitner and Pettus (1963), and since then Brown (1966) extended the known geographic range from there into the nearby Snowy Range, which is approximately 150 miles from Little Box Elder Cave (Fig. 2). Spencer and Pettus (1966) found Microsorex associated with wet coniferous forests, in a dry-moist microhabitat; its apparent absence from the Laramie Mountains indicates that arid habitats have developed there.

Orders Chiroptera and Primates.—The fossil bats reported from the cave are all found in the same region today (Long, 1965; Jones, 1964; Jones and Genoways, 1967). Bats, being highly mobile, are not so useful as other mammals for studies in zoogeography. The

same is true for man, represented by a single specimen in Little Box Elder Cave.

Order Lagomorpha.—The pika, Ochotona princeps, is a valuable fossil from the cave. Pikas are not confined to high or cold habitats as Anderson (1968) and other authors have affirmed. In southwest Wyoming and in other states pikas occur in rock piles, in low (warm) or high (cold) habitats. However, the pika, as well as the shrew Microsorex, is absent from the Laramie Mountains today but is present 150 miles southward in the high Snowy Range (Fig. 2).

Order Rodentia.—Some Recent rodents are conspicuously absent from Little Box Elder Cave. The chances of preservation being low for some species may account for their absence (perhaps harvest mice, Reithrodontomys), but it is difficult to appreciate why species as common today as the kangaroo rat, Dipodomys ordii, and the grasshopper mouse, Onychomys leucogaster, are absent in the cave. The jumping mice Zapus princeps and Z. hudsonius are not reported from the cave but occur near the area today, in moist meadows.

Jones (1964) postulated a distribution for the pack rat, *Neotoma floridana*, ranging through Nebraska to the border of present-day Wyoming in the climatic optimum. The absence of *N. floridana* from Little Box Elder Cave is consistent with his hypothetical distribution.

The heather vole, *Phenacomys longicaudus*; rock squirrel, *Spermophilus variegatus*; and meadow vole, *Microtus pennsylvanicus*, reported from the cave have apparently retreated from the cave area. *S. variegatus* and *M. pennsylvanicus uligocola* are known from northern Colorado, and *Phenacomys* is found in the Snowy Range (Fig. 2). Other subspecies of *M. pennsylvanicus* occur in northern Wyoming.

The fossil lemming *Dicrostonyx* (Anderson, 1968; Guilday, 1968a), probably *D. torquatus*, indicates a formerly cold climate.

Today Dicrostonyx is found only in the far north.

Order Carnivora.—The fossil canids are found in the same region today, except the wolf, *Canis lupus*, which, in this century, has been extirpated there by man. The fossil *Vulpes vulpes* indicates that the red fox has inhabited the Central Rockies since late Pleistocene. The large size of the fossil fox resembles that of the Recent prairie subspecies *V. v. regalis* more than the smaller *V. v. macroura* which inhabits the Rockies (Long, 1965). The prairie subspecies may have retreated slightly eastward (Goshen County, Sand Hills Division) as did the shrew *Cryptotis*.

The Mustelidae are well represented from Little Box Elder Cave. Most of the fossil musteline species are present today, although the black-footed ferret, *Mustela nigripes*, is exceedingly rare if still present. Hershkovitz (1966) reported a sight record near Casper, Wyo.

The pine marten, *Martes americana*, is another species that possibly retreated southward slightly from the Little Box Elder Cave region. The marten may occur in the Laramie Mountains; it is known from the nearby Snowy Range but not from the Black Hills

or Bighorn Mountains to the north (Fig. 2). The fossil pine marten indicates former coniferous forest at the cave, as do the records of

Microsorex and Phenacomys.

Long (1965) reviewed the status of the wolverine Gulo gulo (=G. luscus) in Wyoming, where it is known only from the north-western counties. However, Jones (1964) reported Recent Gulo from Scotts Bluff County, in nearby western Nebraska. His record discredits Anderson's hypothesis that Gulo gulo retreated northward in Wyoming because of warming temperature.

Anderson's specimen of *Taxidea* is of a huge badger (length of skull, 143.3 mm; zygomatic breadth, 94.4 mm), slightly larger than the largest Recent specimens I have observed. Her specimen is significantly larger than those obtained in modern times from eastern Wyoming. A specimen from Pawnee Creek, Neb., of Pleistocene age.

is likewise large (Cook, 1931).

Anderson (1968) was apparently unaware of Long's (1964) new name combination, Taxidea taxus marylandica, for a badger from Cumberland Cave, Md. This taxonomic assignment was made because the Maryland specimen (1) differed slightly from specimens of all the Recent subspecies, but (2) was doubtless capable of interbreeding with any of them. Furthermore, the assignment worked a nomenclatural compromise between those taxonomists who emphasized the former condition and those who recognized the latter. Badgers have retreated generally westward from Maryland, New York, and Kentucky since the Pleistocene (Long, 1964; Guilday, 1968b).

Of interest is the apparent absence of the spotted skunk, Spilogale. Long (1965) hypothesized that Spilogale putorius gracilis and S. p. interrupta approached each other interacting as species in eastern Wyoming after the extensive glaciations of the Pleistocene. He reported that specimens of both spotted skunks were taken sympatrically from the same trap at Iron Mountain, in Laramie County, Wyo. Mead (1968) found that these spotted skunks have different reproductive patterns and appear to be isolated reproductively by a temporal mechanism. Jones (1964:29) found all Nebraskan Spilogale referable to interrupta and hypothesized that it dispersed westward

through Nebraska.

The felids in Little Box Elder Cave are found today in this region except that *Panthera atrox* is extinct and the mountain lion, *Felis concolor*, has been drastically reduced in numbers by man.

Orders Perissodactyla and Artiodactyla.—The records of two Pleistocene horses, in Little Box Elder Cave, may indicate a strong prairie influence (in the climatic optimum?). Camelops and Tanupolama are interesting records of camelids now extinct in North America. Most of the remaining fossil artiodactyls are found in the region today. The mountain sheep, Ovis canadensis, has been locally extirpated. However, the mountain goat, Oreamnos, is now known only far to the north except for man-made introductions into the Yellowstone area (Long, 1965). The tentatively identified Symbos

(p. 18) is now extinct. The questionable specimen of *Alces alces* is interesting because the moose occurs now no closer to the cave than the Wind River Mountains in western Wyoming (Fig. 2).

Past Ecological Requirements.—There are problems in understanding past climatic and other ecological conditions on the basis of such a heterogeneous mixture of boreal and warmth-adapted taxa as found in Little Box Elder Cave. It is not accurate to state that Dicrostonyx occurs in cooler habitats than those found in Wyoming today, because the Hudsonian and Arctic-alpine life-zones are wide-spread, even if narrow, in the Rockies. It is now obvious that some of the fossil forms reported as "boreal" (e.g., Gulo, Phenacomys, Eutamias, Ochotona) are not always confined to boreal zones. Finally, the presence of both warmth-adapted and boreal species mixed together (e.g., Cryptotis and Dicrostonyx) is not easily construed as an ecological succession in which the former replaces the latter. Unfortunately, the remains have not been carbon-dated, but the boreal species reportedly did predominate in the lower strata so far excavated in the cave.

Other evidences (zoogeographical, geological, paleontological) from other places suggest that the cold Wisconsin climate moderated, and that it even became warmer than present. Animal distributions (Long, 1965; Jones, 1964) provide evidences for reconstructing the ecological history of this study region. For example, it is quite reasonable to assume that when the climate was warmer than at present *Cryptotis* might have rapidly expanded its range westward in the narrow riparian habitats along the Platte River as far as Little Box Elder Cave, and subsequent cooler climate may have caused this species to withdraw to its present position. This explanation is the simplest in view of the Recent mammalian distributions and ecologi-

cal requirements of the mammals.

SUMMARY AND CONCLUSIONS

Anderson's conclusion (1968:52) and my own (Long, 1965:733) that some coniferous forests occurred in what are now arid lowlands is derived from studies of the fossils in the first case and numerous Recent animal distributions in the second. This conclusion is reinforced by palynological studies from nearby areas (Hansen, 1951; Watts and Wright, 1966). The hypothesized effects of alpine (Long, 1965) and continental glaciations (Jones, 1964) on mammal distributions in the region are supported by Anderson's paleontological findings. The presence of cold-adapted species such as *Dicrostony:x* and *Oreamnos* indicate that the climate was formerly colder (also indicated by geomorphic studies on alpine and continental glaciations). Anderson suggested that these boreal mammals and others have retreated northward as the climate warmed, and a relict Recent population of *Lepus americanus* from the Bighorn Mountains suggests the same thing.

The presence of several fossil species substantiates Jones's (1964) hypothesis that some mammals on the Great Plains were affected

by the climatic optimum. Some mammals have retreated southward and eastward since this very warm period. The withdrawal of several boreal taxa from the cave area apparently resulted from an abrupt amelioration of cold climate. Several lowland mammals (e.g., Cryptotis, Spermophilus variegatus) apparently overextended their boundaries for the climate of Recent time and were extirpated in the Laramie Mountains.

The fossil remains in the Little Box Elder Cave not only substantiate to some extent several zoogeographical hypotheses about Wyoming and Nebraskan mammals, but also provide important evidence which, when used with zoogeographical evidence, suggests that at least along the eastern margin of the Rocky Mountains the warm climatic optimum altered and influenced the distribution of some Rocky Mountain mammals.

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